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The role of dispersal mechanisms, regenerative strategies and seed banks in the vegetation dynamics of the British landscape

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3.1 Introduction

Modern land uses, particularly those related to agriculture, have fundamentally reshaped the vegetation of the United Kingdom. The development of machinery for ploughing, earth-moving, timber felling and drainage, and the increased use of fertilisers and herbicides have transformed much of the relatively unproductive landscape exploited by our ancestors into the intensively managed rural and urban areas with which we are now familiar. Today, in many lowland areas, only small, isolated fragments of ancient habitat remain, and land use has emerged as the most important determinant of plant distribution in the contemporary British landscape (Hodgson 1986a, b). Indeed, it is estimated that the majority of species in the British flora are less common than formerly as a direct consequence of modern land use (Hodgson 1987a). However, the build-up of agricultural surpluses has resulted in a radical rethinking of agricultural policy, and initiatives such as 'set-aside' and 'extensification' are being developed to reduce agricultural production. This development provides the potential, at least in theory, for an expansion of some of the many plant species whose abundance has declined as a result of modern agriculture.

Unfortunately, our ability to predict which species will be able to take advantage of any reduction in the intensity of land use is restricted. First, the practical effects of new agricultural policies on land use are uncertain (see Harvey and Bell, below, pp. 256–73). Second, despite the pioneering studies of Ridley (1930), Salisbury (1953) and van der Pijl (1982), we have an inadequate appreciation of the dispersal and colonising abilities of species.

Colonisation of new locations may result from (i) an influx of seed or other plant propagules from another site; or (ii) recruitments from a persistent seed or spore bank which has survived *in situ* and is a relict of a previous vegetation type and management regime. However, in a rapidly changing and heavily disturbed landscape, such as that of lowland Britain, this simple dichotomy

may not capture all of the detail necessary to devise useful predictions of colonising potential. In this chapter, therefore, our enthusiasm for dispersal theory will be tempered by a concern to examine field evidence of what is actually taking place. First, the strategies which appear to have evolved under selection pressures related to dispersal in space and time will be analysed using parts of the theoretical framework of Grime (1979) and the autecological data for common British flowering plants presented by Grime, Hodgson and Hunt (1988). This analysis permits comparison of the extent to which plants present in different habitats have different mechanisms of dispersal. Second, we consider the importance of different vectors (e.g. animals, wind and water) in these various habitats. Third, the success of the mechanisms and vectors in contemporary landscapes will be assessed. The results of these three separate analyses will then be used to predict the changes to the flora of the British countryside which may result from set-aside and extensification.

3.2 An analysis of the relationships between habitat and dispersal mechanisms in common British plants

3.2.1 Ecological theory

3.2.1.1 DISPERSAL IN TIME

Regeneration involving a bank of persistent seeds or spores (B$_s$)

Mechanisms by which some seeds or spores persist in the soil for over one year, and usually for considerably longer periods, provide a means for survival in habitats subject to spatially predictable but infrequent episodes of disturbance. If there is a high degree of habitat continuity, as in heathlands exposed to occasional burning, species (e.g. heather (*Calluna vulgaris*)) tend to accumulate a large and long-persistent Type IV seed bank (*sensu* Thompson and Grime 1979) (see Figure 3.1).

Where the habitat is more transient (e.g. a spoil heap), species tend to combine the potential for rapid expansion of populations with a capacity for persistence as dormant seeds, when conditions are unfavourable for colonisation (see Grime *et al.* 1988). Such species often have a small but persistent seed bank (SB III – Figure 3.1). Species with a Type III seed bank include annual- and rough-stalked meadow grass (*Poa annua* and *P. trivialis*), which are among the first colonists during the process of 'sward deterioration' in sown grasslands (Morrison 1979).

Other species, which are not considered to show dispersal in time, produce seeds which either germinate shortly after being shed – Type I seed bank (e.g. rye-grass (*Lolium perenne*)) – or the following spring – Type II (e.g. sycamore (*Acer pseudoplatanus*)) (Figure 3.1).
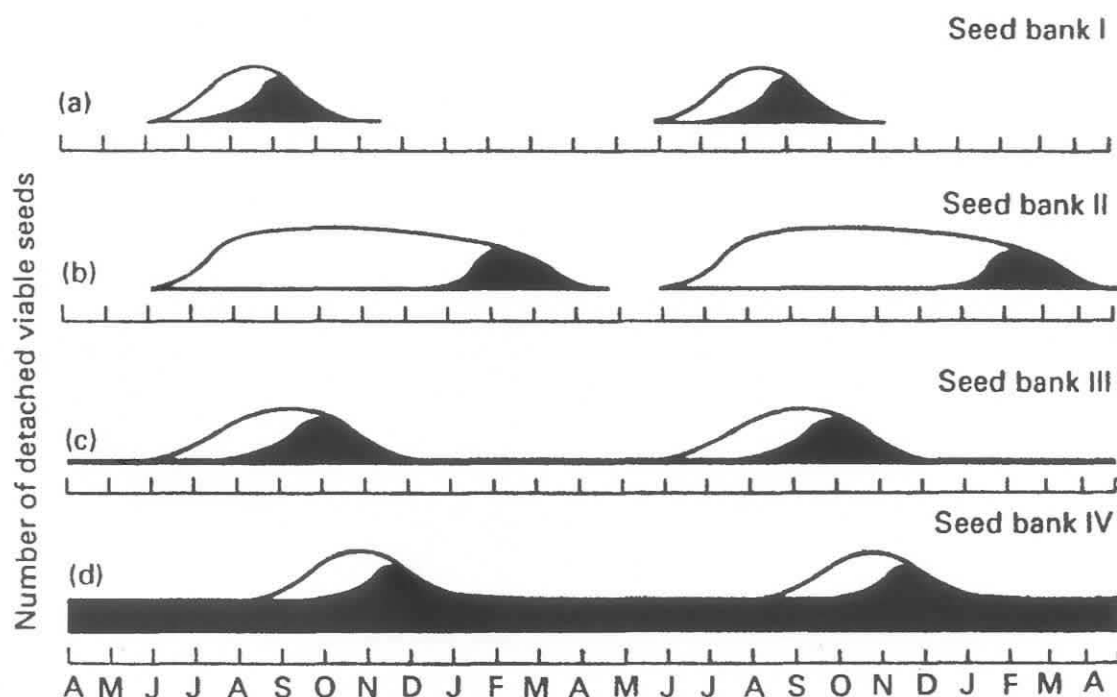
Figure 3.1   Scheme describing four types of seed banks of common occurrence in temperate regions. ■ Seeds capable of germinating immediately after removal to suitable laboratory conditions. □ Seeds viable but not capable of immediate germination (from Grime 1979).

Regeneration involving persistent juveniles (Bⱼ)

In mature, relatively undisturbed and unfertilised forest or grassland, an equilibrium may be established such that annual production is low despite the continuous vegetation cover, and the majority of the plant populations consist of long-lived individuals. In such circumstances, opportunities for establishment from seed are scarce and the most important mechanism of regeneration is often that which depends on persistent juveniles. In species with this strategy, the seed bank is short-lived, but the seedlings and immature individuals (often in a very stunted condition) are capable of surviving long periods in which little or no growth is possible. Further growth of these juveniles often occurs in several episodes which depend upon the formation of local gaps within the neighbouring vegetation. The agency of gap creation may be, for example, an animal's hoof print or, in woodland, the death of a neighbouring tree.

The recognition of a bank of persistent juveniles is dependent upon detailed demographic studies, and few examples of this probably widespread strategy have been documented. Among those which have received attention are those of sanicle (*Sanicula europaea*) (see Tamm (1956) and Inghe and Tamm (1985)) and trees such as ash (*Fraxinus excelsior*) and sycamore.

3.2.1.2 DISPERSAL IN SPACE

Production of numerous widely dispersed seeds or spores (W)

Species with this strategy produce many thousands of small, usually wind-borne propagules. They are well equipped to colonise habitats which are relatively inaccessible (e.g. cliffs) or which are subject to spatially unpredictable disturbances, such as those resulting from road and building construction. Rose-bay willow-herb (*Chamerion angustifolium*) has this dispersal mechanism.

Table 3.1   Strategies of dispersal – summary table

	Arable	Pasture	Skeletal	Spoil	Wasteland	Wetland	Woodland
W	(−)	−	(+)	+	−	(+)	−
B_s	+	(−)	(−)	+	(−)	+	−
SBIII/IV	(−)	(−)	+	+	(−)	(−)	−
Veg	(+)	−	−	(+)	−	+	(−)
None	−	+	(+)	−	+	−	+

Notes: + Statistically significant positive association
         (+) non-significant positive association
         (−) non-significant negative association
         − statistically significant negative association
         Strategies abbreviated as in Figure 3.2

3.2.1.3 A FURTHER DISPERSAL MECHANISM

Field observations suggest that the range of strategies outlined above is inadequate to represent the major dispersal mechanisms currently operating in central England. Species from such diverse habitats as ponds (e.g. Canadian pondweed (*Elodea canadensis*)), river margins (e.g. monkey flower (*Mimulus guttatus* × *luteus*)), lawns (e.g. slender speedwell (*Veronica filiformis*)), forestry rides (e.g. trailing tormentil (*Potentilla anglica* × *reptans*)) and gardens (e.g. *Oxalis corymbosa*) have all become widely dispersed within the region, despite an inability to produce seed. Their spread appears to have resulted from the dispersal of vegetative fragments through the agency of man, machinery or water. However, this capacity for vegetative spread is by no means exceptional. Experimental studies on the capacity of cuttings to root (Hodgson and Camm, unpublished) indicate that many fully fertile species are equally able to regenerate from detached portions of shoot. This capacity to root from cuttings, although very much a feature of species from disturbed habitats, is not found in related species from more stable situations. It appears to be of adaptive significance, both as a means of recovering after damage *in situ* and as a means of dispersal. Accordingly, a further dispersal

mechanism, 'population expansion and long-distance dispersal by vegetative means' (VEG), has been included in the analysis. This mechanism refers to species where vegetative regeneration is more important than regeneration by seed or spore for both local consolidation of established populations and dispersal to new sites.

3.2.2 Materials and methods

In order to ascertain the relationship between mechanisms of regeneration and habitat type, information of three kinds was abstracted from Tables 6.1 and 6.3 of Grime *et al.* (1988) for 259 common British species:

1   abundance in each of the seven major habitats recognised for inland Britain (wetland, skeletal, arable, spoil, pasture, wasteland and wood-land);
2   regenerative strategy;
3   seed bank type.

The extent to which particular mechanisms of regeneration are characteristic of the flora of the different major habitats was then assessed. A comparison was also made of the flora of rye-grass pastures (resulting from modern agriculture) and that of other (typically older) types of pasture. Information was insufficient to allow analysis of the distribution of species forming banks of persistent juveniles. To avoid comparisons between species of extremely disparate form or life cycle within the same analysis, tall (>2 m) woody species and ferns were omitted.

3.2.3 Results

The results illustrated in Figure 3.2 and summarised in Table 3.1 indicate that particular strategies of dispersal in space and time differ markedly in frequency according to habitat. Species associated primarily with arable land, spoil and wetlands tend to possess strategies facilitating dispersal in space (W, VEG) and/or time (B_s). In contrast, pasture, wasteland and woodland contain a relatively small proportion of species with attributes which can be reliably identified with dispersal in space and/or time (Figure 3.2, Table 3.1). Many of these species which are without any obvious dispersal mechanism are found in unproductive habitats (Figure 3.3). The skeletal habitat appears intermediate between the two groupings, in that the component species may have a capacity for dispersal in space (W) but, in other respects, they resemble the second, under-dispersed grouping.

Although persistent seeds are characteristic of arable, spoil and wetland, some differences in seed bank type can be detected between the three habitats. On spoil heaps, which may only provide a transient habitat, most species have a small, Type III seed bank. However, in arable and wetland habitats,
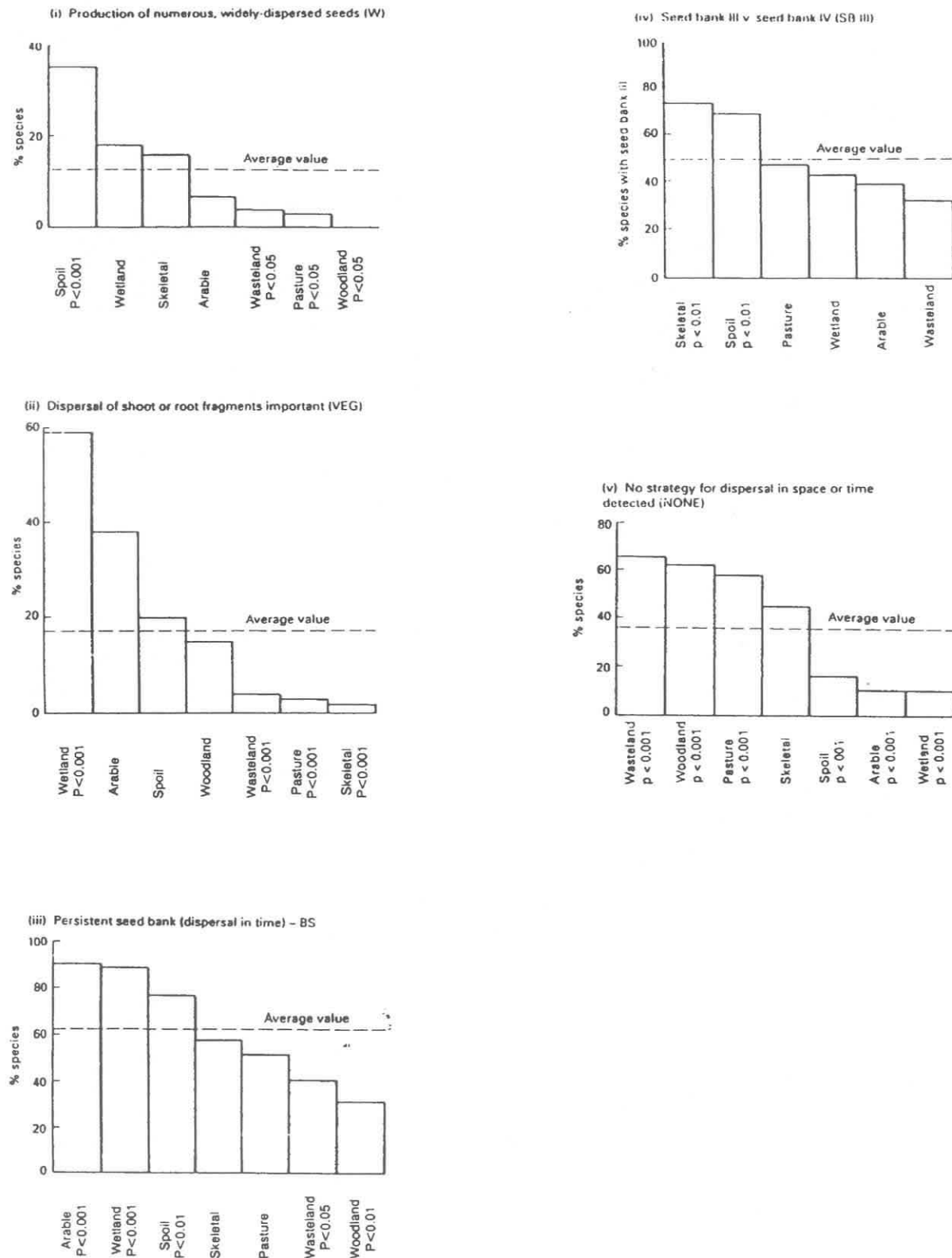
Figure 3.2   The strategies of dispersal in space and time of common species of the six major habitats of inland Britain. Data have been abstracted from Grime *et al.* (1988). The calculations in (iv) refer only to species with a persistent seed bank. Statistical comparisons of the values for species common in each habitat and those infrequent and uncharacteristic of the habitat were carried out by means of 2 X 2 contingency tables. Where χ^2 was statistically significant, the level of this significance is appended to the diagram.

which are often more permanent, many species accumulate a Type IV seed bank (Figure 3.2).

These analyses represent something of an oversimplification. Some plant communities differ considerably from the mean values for the major habitat grouping under which they are classified (Figure 3.4). Thus, in recent rye-grass meadows and pastures, the most frequent colonists tend to exhibit strategies facilitating dispersal in space (W, VEG) and/or in time (B_s), unlike the remainder of pasture species. They also show a more pronounced tendency to form a Type III rather than a Type IV seed bank. Thus they are similar in their dispersal characteristics to species which colonise spoil heaps.

3.2.4 Conclusions

As predicted by ecological theory, the range of dispersal strategies present in the flora is a reflection of the permanency and degree of disturbance characteristic of the habitat. The flora of impermanent disturbed habitats (e.g. spoil heaps, rye-grass pasture) has well-developed mechanisms of dispersal in space and time. In more permanent disturbed habitats (e.g. arable land and wetlands subject to flooding), a large persistent seed bank (facilitating dispersal in time) is frequently prominent. Species of more permanent, less-disturbed habitats (e.g. permanent pasture and woodland) tend to show
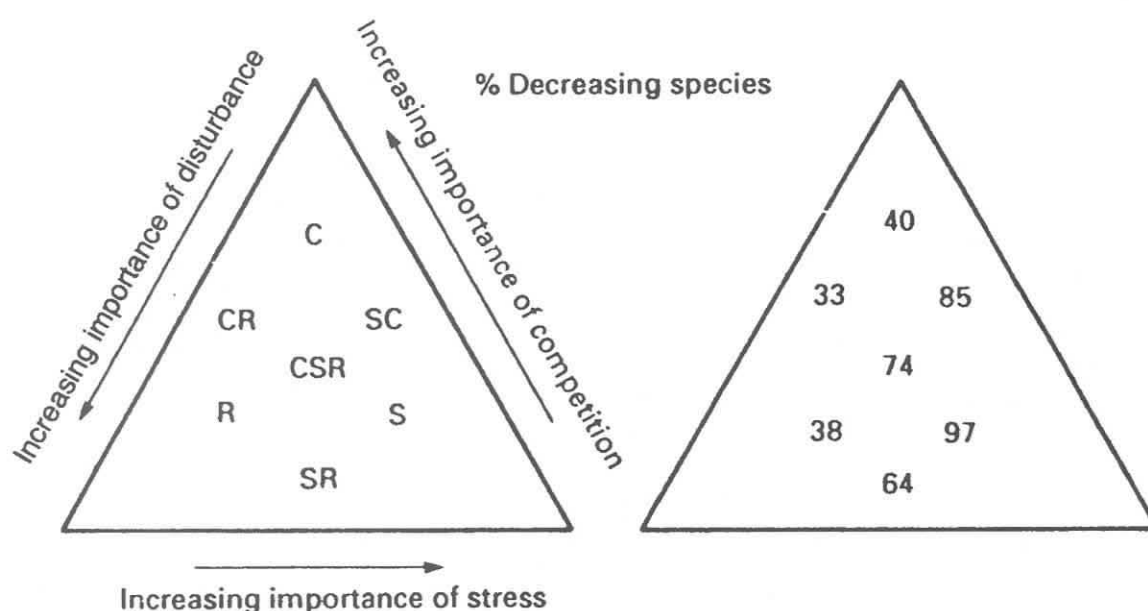

Figure 3.3   The distribution with respect to plant strategy *sensu* Grime (1974) of species for which no strategy for dispersal in either space or time was detected. Values refer to the percentage of species of this type within each category of plant strategy.
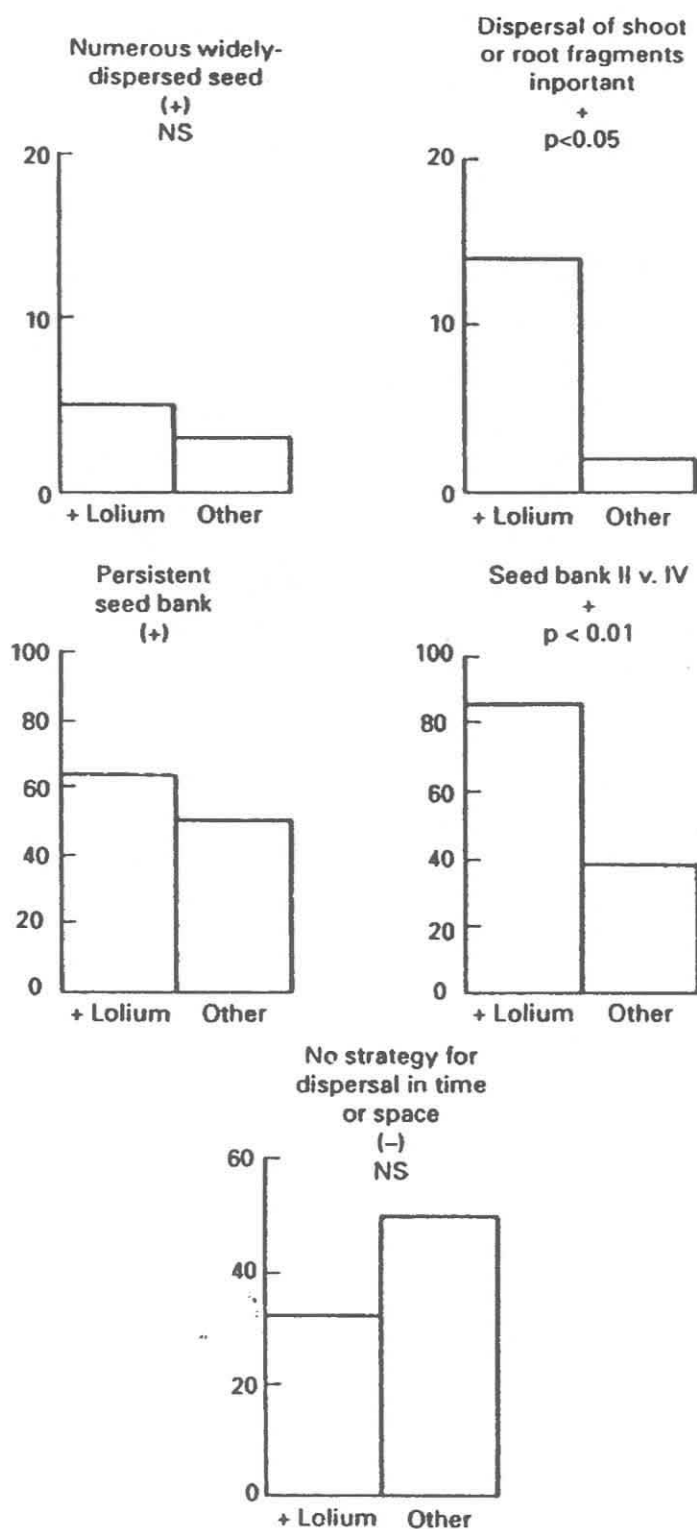
Figure 3.4   A comparison of the strategies of dispersal of common species of rye-grass (*Lolium perenne*) pasture and those characteristic of other pasture types. Inclusion in the rye-grass pasture category was dependent upon the species' occurrence in >20 per cent of the pasture samples in which rye-grass had a rooted frequency of ≥50 per cent. Commonly sown species (e.g. white clover (*Trifolium repens*)) were, however, omitted. Species were classified by reference to the survey data utilised in Grime *et al.* (1988). Statistical tests, using χ^2, are as in Figure 3.2 and, following the conventions of Table 3.1, a strategy more characteristic of species of rye-grass pastures is identified by a '+', while that with a negative association is given a '−'.

no obvious mechanisms of dispersal in time and space. However, many of these species which lack an obvious dispersal mechanism are associated with unproductive habitats, and form, we suspect, a bank of persistent juveniles.

3.3 An analysis of the relationship between habitat and vector of dispersal

3.3.1 Ecological theory

Past studies of dispersal have generally been addressed rather narrowly to the process of seed dispersal in space. The benefits of a broader approach, which considers the full range of reproductive strategies for dispersal in time as well as space, are hopefully apparent from the preceding section. Nevertheless, in deference to the large volume of valuable research which has been devoted to the vectors of seed dispersal (eg van der Pijl 1982), the agency by which seeds are dispersed in the different habitats will also be considered here.

3.3.2 Materials and methods

Unfortunately, the classification of dispersal types adopted here is only approximate, because it is based primarily on an analysis of the morphology of dispersules and not on observations of dispersal in the field.
    The following classification of vectors of dispersal has been adopted:

1   dispersal by wind (seeds plumed (e.g. dandelion (*Taraxacum* agg.)), winged or strongly flattened (e.g. sycamore or minute (e.g. orchids));
2   dispersal by water (seeds and/or fruits and/or seedlings float and plants typically found growing beside, or in, water (eg yellow water-lily (*Nuphar lutea*));
3   dispersal by animals (seeds within a fleshy fruit (e.g. blackberry (*Rubus fruticosus*) or seeds or fruits adhesive (e.g. goosegrass (*Galium aparine*));
4   dispersal unspecialised (includes all species not classified in the previous three categories and will inevitably include species which are genuinely poorly dispersed and those whose adaptations for dispersal are not immediately apparent from the morphology of the seed or fruit).

3.3.3 Results

The main vector of seed dispersal appears to differ according to habitat (Figure 3.5), although in some habitats (e.g. arable) a majority of species have no well-defined morphological adaptations facilitating dispersal in space. Dispersal by wind, which includes many species which produce
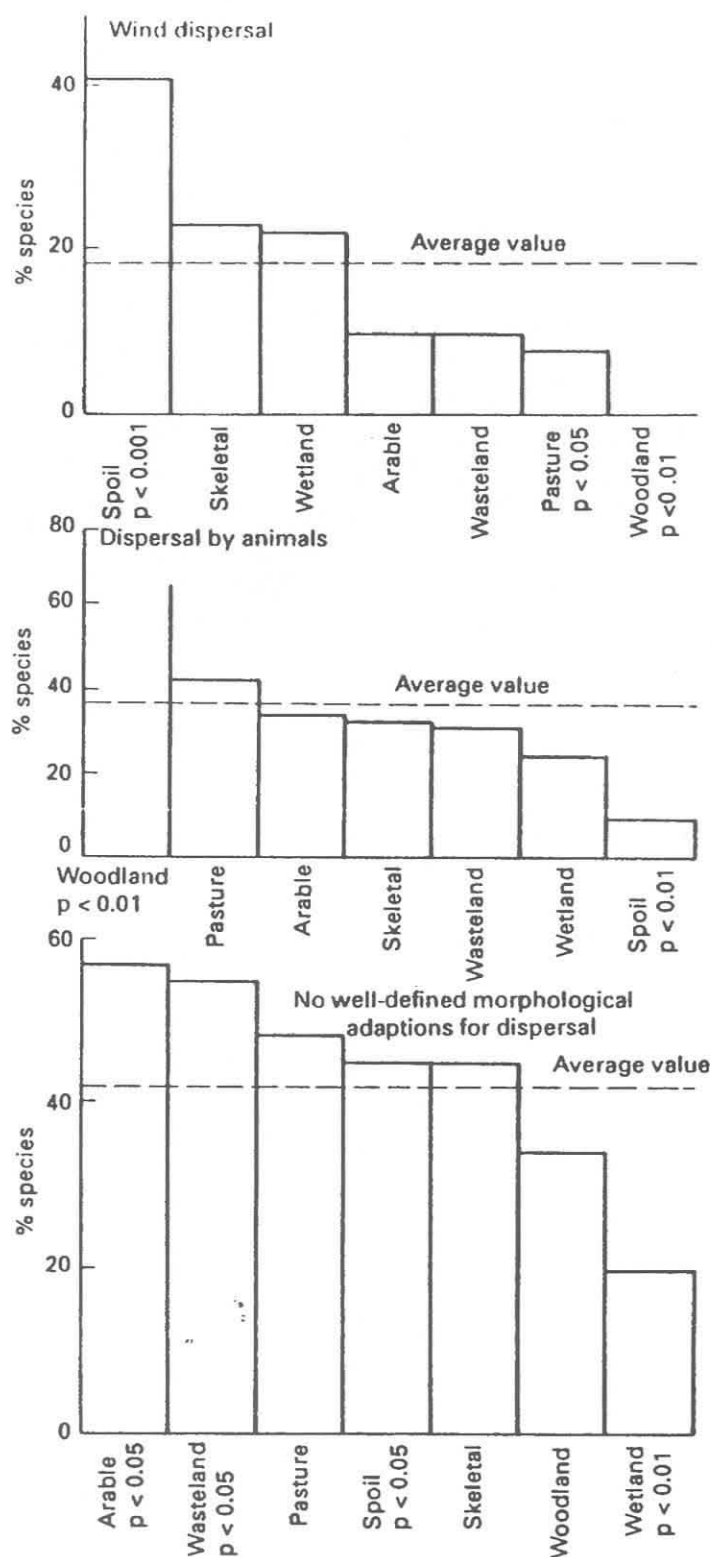
Figure 3.5   The vectors of seed dispersal of common species in the six major
             habitats of inland Britain. In addition to the mechanisms described
             here, 41 per cent of wetland species are dispersed by water. Sources
             of data and statistical tests are as in Figure 3.2.

             NB As the classification of dispersal types is based primarily on
             morphological characters, certain attributes of importance in dispersal
             (e.g. the presence of a thick seed coat, which may allow the seed to pass
             unharmed through the digestive tract of an animal) will not have been
             detected. Thus, a proportion of species in the 'unspecialised' category
             will be misclassified.

numerous widely dispersed seeds or spores (dispersal strategy W), is most typically associated with spoil. In contrast, the strategy is poorly represented in woodland, wasteland, pasture and arable land. Dispersal by animals shows an opposite relationship, a positive association with woodland and a negative one with spoil.

3.3.4 Conclusions

Abiotic vectors for dispersal (wind) are particularly associated with disturbed, impermanent habitats (e.g. spoil). Only in more stable habitats (e.g. woodland) does dispersal by animals become more important.

3.4 The mechanisms and vectors for dispersal of increasing and decreasing species

2.4.1 Ecological theory

Modern land use has transformed the floristic composition of both the rural and urban areas of the United Kingdom, and a majority of species has probably decreased in abundance (see Hodgson 1987 a, b). Policies such as set-aside and extensification are only likely to reverse this trend if suitable habitats are created and if decreasing species can re-establish themselves. The probability of recolonisation by widespread but decreasing species will now be addressed by comparing the dispersal mechanisms and vectors of increasing and decreasing species. A difference between the two groups of species might imply an impaired ability for the natural colonisation of decreasing species.

3.4.2 Materials and methods

The extent to which species with different mechanisms and vectors of dispersal are increasing or decreasing has been assessed using Tables 6.1 and 6.3 of Grime et al. (1988). For simplicity of presentation, the whole data set has been included in the analysis. However, analysis of individual habitats (Hodgson and Grime, unpublished) suggests that the results are relevant to each major habitat.

3.4.3 Results

Species which are currently increasing tend to have strategies favouring dispersal in space (W, VEG) and time (B_s), while decreasing species do not (Figure 3.6). Also, abiotic dispersal of seeds by wind is favoured rather than
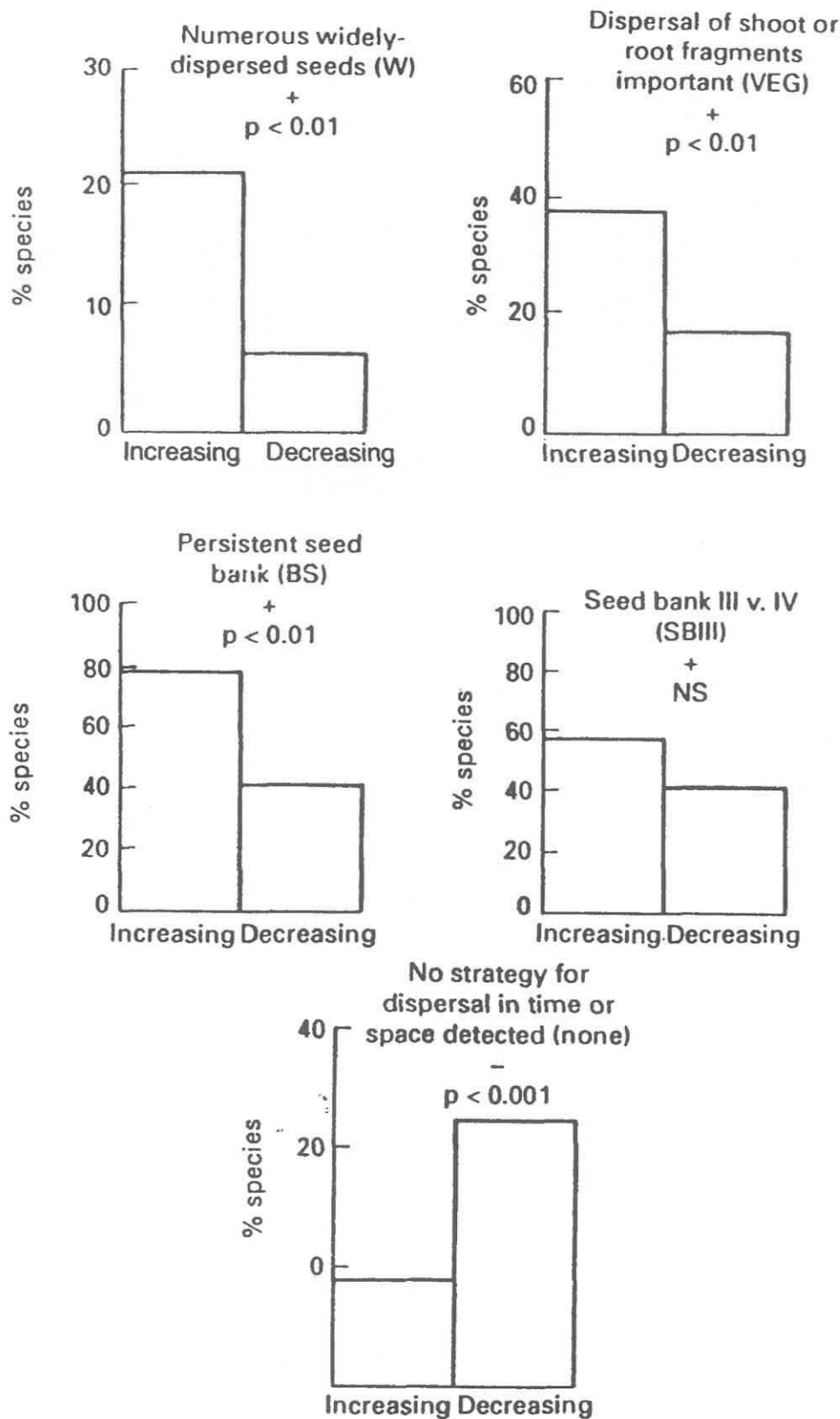
Figure 3.6   Review of the success in contemporary landscapes of different
dispersal strategies. Estimations as to whether species are increasing
or decreasing have been abstracted directly from Grime *et al.* (1988).
Statistical tests are as in Figure 3.2 and, following the conventions
of Table 3.1, a strategy more characteristic of increasing species is
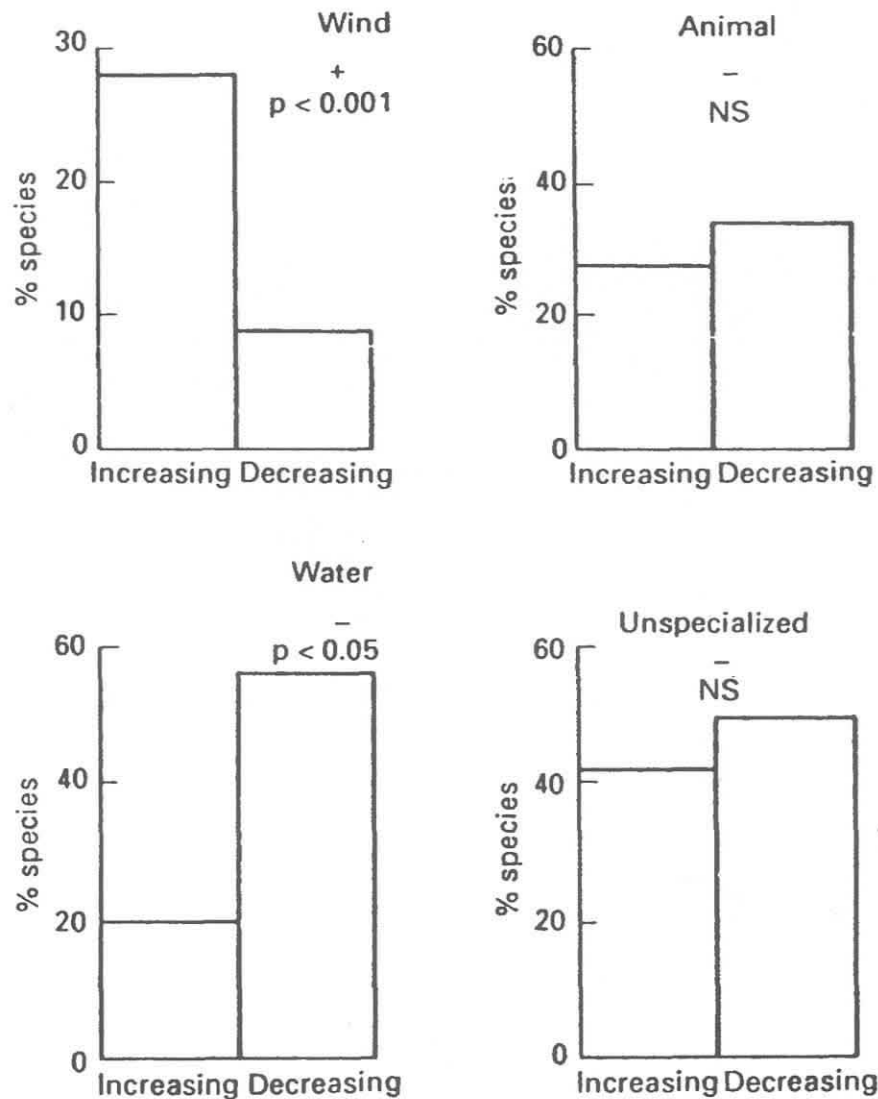indicated by a '+' and one associated with decreasing species by a
'−'.

Figure 3.7 Predictions of the success in contemporary landscapes of different methods of seed dispersal. Sources of information and conventions as in Figures 3.2, 3.5 and 3.6.

animal dispersal (Figure 3.7), although another means of abiotic dispersal (water) appears unfavourable.

3.4.4 Conclusions

The results indicate that, because of the disruptive effects of modern land use, there are strong selection pressures within the British flora for dispersal ability. Species with mechanisms and vectors favouring effective dispersal tend to be increasing, while those lacking obvious dispersal mechanisms, including, we suspect, many species with a persistent bank of juveniles, tend to be decreasing.

3.5 Discussion

3.5.1 The relative importance of dispersal and other factors

The patterns apparent within the data set, and illustrated in Figures 3.1–3.7, are explicable in terms of contemporary ecological theory, with the dispersal mechanisms and vectors of species reflecting the permanence, and vulnerability to disturbance, of their habitats (Figures 3.1–3.7). Species from impermanent or disturbed habitats tend to have well-defined mechanisms of dispersal in space and/or time; those from more stable habitats do not. Moreover, the high level of disturbance, which is so much a feature of modern agricultural practice and of urban and industrial development, favours species with well-developed mechanisms of dispersal in space and/or time (Figure 3.6). Equally significant is the prevalence in unproductive habitats of species with no apparent mechanism of spatial or temporal dispersal (Figure 3.3). This apparent lack of a dispersal mechanism, coupled with an association with unproductive habitats, is characteristically associated with regeneration by persistent juveniles. These species tend to be decreasing and many are relicts of the less intensively managed landscapes of our ancestors.

The results are calculated from the largest available ecological data set for the British flora. Inevitably, however, the classification of dispersal mechanisms and vectors used here is both provisional and incomplete, and interpretation is particularly hampered by the absence of reliable field data on the occurrence of banks of persistent juveniles.

Another important point can be appreciated by reconsidering vectors of dispersal. Abiotic dispersal by wind is favoured rather than dispersal by animals in disturbed landscapes. However, abiotic dispersal by water does not appear advantageous, even though dispersal by water is clearly a very effective mode of dispersal within the area being studied (Grime et al. 1988). This apparent anomaly appears to relate to the fact that wetlands are particularly vulnerable to eutrophication and drainage, and, as a result, many wetland species are declining (Hodgson 1986a). Dispersal must be considered in conjunction with other aspects of the ecology of the species. As illustrated by Figures 3.2–3.7, there are many exceptions to the trends identified, and it must be emphasised that, irrespective of the dispersal strategy, a species will only be successful if the plant itself is capable of exploiting the habitat to be colonised.

The contemporary abundance of productive habitats is without precedence in the evolutionary history of the British flora, and many underexploited niches probably still remain in the range of productive habitats created by modern land use (Hodgson 1987b). This may explain the success of aliens such as Japanese knotweed (*Reynoutria japonica*), whose tall (1.5–2.0 m), dense leaf canopy and vigorous lateral vegetative spread appear to make it more competitive than most native species exploiting similar, undisturbed, productive habitats. The absence of seed production and the requirement for

root fragments to be dispersed, typically by human agencies, appear to have been only a minor handicap to the spread of the species.

More generally, Salisbury (1953), studying the spread of aliens, argues that rapid rates of colonisation are more likely once a species has exceeded some critical level of abundance. In support of this 'infection pressure' hypothesis, Grime 1986 suggests that transport in soil or by other means is sufficient to ensure colonisation of spoil, provided that the output of disseminules is sufficiently high. These conclusions are probably equally relevant to the highly disturbed, arable and pastoral habitats created by modern agriculture. Thus, the colonising ability of an individual species (the product of both dispersal and subsequent establishment) should not be assessed simply by reference to strategies of dispersal. The dispersal strategy may give a clue, but other facets of the biology of the species must also be considered.

3.5.2 Implications for future land use

Because efforts are being made to reduce agricultural production, the impacts of two possible scenarios, abandonment and less intensive management, upon species recruitment will now be considered.

Abandonment will generally result in the formation of scrub or woodland, and, because relatively few trees, shrubs and woodland herbs and grasses form persistent seed banks (Grime et al. 1988; Figure 3.2), dispersal in space is likely to be a critical factor in the colonisation process. The lack of mobility of many woodland species, however, means that the community which develops under these circumstances will lack many of the species characteristic of older woodland (see Peterken 1981).

The effect on species composition of reducing the intensity of management is less easy to predict. However, the problems involved can be illustrated by examining the colonisation of productive pasture after the cessation of fertiliser additions and reseeding. Initially, and possibly for a considerable time, the high productivity of the site will restrict the range of species for which establishment is possible. However, even following a reduction in productivity, there are additional constraints relating to dispersal. First, the number of species of less productive habitats in the seed bank and their overall contribution to it may be small. Second, we suspect that many species of unproductive grassland habitats lack obvious strategies of dispersal in space and time, other than the formation of a bank of persistent juveniles (B_j) – see Figures 3.2 and 3.3. Thus, they are unlikely to be effective colonists of new sites, particularly if these sites are some distance away. The 'seed rain' on a site appears to be made up mostly of species which occur in the immediate vicinity (Huby 1981; Quinn and Robinson 1987; Jefferson and Usher 1989), and the distance of sites from patches of existing, more ancient, vegetation can greatly affect the species richness obtained after colonisation (Jefferson and Usher 1986).

There are two critical differences between the habitats typical of older 'traditional' agriculture and modern forms: level of productivity, and extent

of habitat continuity. As illustrated by the results in Figures 3.2–3.4, many of the more ancient pastoral ecosystems are characterised by species both associated with unproductive habitats (stress tolerators, *sensu* Grime 1974) and with little capacity for dispersal in time and/or space, other than by means of a bank of persistent juveniles (B_j). In contrast, species from modern habitats usually have more rapid growth rates (see Grime and Hunt 1975) and, as a result of human activities, tend to be widely dispersed.

The well-publicised ability of a few groups of species with widely dispersed seeds or spores (W) (e.g. orchids (Orchidaceae) and club mosses (Lycopodiaceae)) to colonise spoil heaps in urban and industrial areas (see Gemmell 1977) has tended to overshadow the plight of the majority of species from unproductive habitats which lack this regenerative strategy. If policies designed to reduce agricultural production are also to benefit nature conservation, they will need to consider both (1) the optimal siting of areas of low (or zero) intensity agriculture relative to surviving fragments of more ancient vegetation, and (2) the forms of management which will encourage colonisation. Furthermore, because in many areas relatively few of the desirable species of older, less intensive agricultural systems remain, the development of policies and management procedures for species reintroductions is urgently needed.

References

Gemmell, R. P. (1977). *Colonization of Industrial Wasteland*. Arnold, London.

Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature*, 250, 26–31.

Grime, J. P. (1979). *Plant Strategies and Vegetation Processes*. Wiley, Chichester.

Grime, J. P. (1986). The circumstances and characteristics of spoil colonization within a local flora. In M. W. Holdgate (ed.), *Proceedings of the Royal Society Discussion Meeting on Quantitative Aspects of the Ecology of Biological Invasions*, Philosophical Transactions of the Royal Society of London, B314, London, pp. 637–54.

Grime, J. P. and Hunt, R. (1975). Relative growth-rate; its range and adaptive significance in a local flora. *Journal of Ecology*, 63, 393–422.

Grime, J. P., Hodgson, J. G. H. and Hunt, R. (1988). *Comparative Plant Ecology: A functional approach to common British species*. Unwin Hyman, London.

Hodgson, J. G. (1986a). Commonness and rarity in plants with special reference to the Sheffield flora. I: The identity, distribution and habitat characteristics of common and rare species. *Biological Conservation*, 36, 199–252.

Hodgson, J. G. (1986b). Commonness and rarity in plants with special reference to the British flora. II: The relative importance of climate, soils and land-use. *Biological Conservation*, 36, 253–74.

Hodgson, J. G. (1987a). Growing rare in Britain. *New Scientist*, 113 No. 1547, 38–9.

Hodgson, J. G. (1987b). Why do so few plant species exploit productive habitats? An investigation into cytology, plant strategies and abundance within a local flora. *Functional Ecolo.*, 1, 243–50.

Huby, M. (1981). *The natural colonization of colliery spoil.* D. Phil thesis, University of York.

Inghe, O. and Tamm, C. O. (1985). Survival and flowering of perennial herbs. 4: The behaviour of *Hepatica nobilis* and *Sanicula europaea* on permanent plots during 1943–1981. *Oikos*, 400–20.

Jefferson, R. G. and Usher, M. B. (1986). Ecological succession and the evaluation of non-climax communities. In M. B. Usher (ed.), *Wildlife Conservation Evaluation*, Chapman & Hall, London, pp. 69–91.

Jefferson, R. G. and Usher, M. B. (1989). Seed rain dynamics in disused chalk quarries in the Yorkshire Wolds, England, with special reference to nature conservation. *Biological Conservation*, 47, 123–36.

Morrison, J. (1979). Botanical change in agricultural grassland in Britain. In A. H. Charles and R. J. Haggar (eds), *Changes in Sward Composition and Productivity*. Occasional Symposium No. 10, British Grassland Society, Maidenhead, pp. 5–10.

Peterken, G. (1981). *Woodland Conservation and Management.* Chapman & Hall, London.

Pijl, L. van der (1982). *Principles of Dispersal in Higher Plants.* Springer-Verlag, Berlin.

Quinn, J. F. and Robinson, G. R. (1987). The effects of experimental subdivision on flowering plant diversity in a Californian annual grassland. *Journal of Ecology*, 75, 837–55.

Ridley, H. N. (1930). *The Dispersal of Plants Throughout the World.* Reeve, Ashford.

Salisbury, E. J. (1953). A changing flora as shown in the study of weeds of arable land and waste places. In J. E. Lousley (ed.), *The Changing Flora of Britain*, pp. 130–39. Buncle, Arboath.

Tamm, C. O. (1956). Further observations on the survival and flowering of some perennial herbs. *Oikos*, 7, 273–92.

Thompson, K. and Grime, J. P. (1979). Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, 67, 893–921.